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Western Spruce Budworm Larval Consumption Rates and Host Foliage Damage

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Western Spruce Budworm Larval Consumption Rates and Host Foliage Damage

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FINAL REPORT

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ABSTRACT

The influence of host species, foliage chemicals, host vigor, sex, instar, and foliage phenology on food consumption and utilization by the western spruce budworm, Choristoneura occidentalis Freeman, was studied. Total foliage ingested was slightly higher for budworms feeding on corkbark fir and white fir when compared to Douglas-fir due to significantly lower efficiency of conversion of ingested foods (ECI) and relative growth rate (RGR) values. Tannin content of the foliage was positively correlated with the amount of foliage ingested and approximate digestability (AD) for budworms feeding on Douglas-fir and negatively correlated with RGR and ECI for those feeding on white fir. Phenols were not correlated with any of the nutritional indices measured. Proteins were positively correlated with pupal weight of larvae feeding on Douglas-fir. Host vigor was positively correlated with relative consumption rate (RCR) and negatively correlated with RGR, ECI, and pupal weight of larvae feeding on corkbark fir. Vigor was positively correlated with RGR and ECI of larvae feeding on Douglas-fir and ECI of larvae feeding on white fir. Female western spruce budworms ingested more foliage, had longer development times, and had greater pupal weights than males. Fifth and sixth instar larvae utilized their food source equally well, but the sixth instar larvae ingested more food due to their larger size. Consumption of early season foliage resulted in normal growth and development, but consumption of middle and late season foliage resulted in retarded development and a high mortality rate.

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Preface

This final report is divided into 4 chapters which represent the 4 publications we anticipate from the research effort. Chapter 1 will be published in: Proceedings CANUSA Workshop Forest Defoliator - Host Interaction: A Comparison Between Spruce Budworm and Gypsy Moth. Chapter 2 will be submitted to Forest Science. Chapters 3 and 4 will probably be submitted to Environmental Entomology. There may be considerable modification in these chapters before they are submitted for publication. Chapters 2-4 also represent Elizabeth A. Blake's Masters thesis.

One of our original objectives (to determine the differences in feeding rates between stands of different defoliation histories) was not accomplished. The reason for this failure was excessive parasitism of larvae used for that part of our study. Throughout this study obtaining parasite-free larvae was a serious problem.

M.R.W., E.A.B.

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INTRODUCTION

Quantitative nutritional studies to determine consumptive rates and nutritional efficiencies have not previously been undertaken for the western spruce budworm, *Choristoneura occidentalis* Freeman. In 1980 this native pest defoliated approximately 1.65 million ha (4.08 million acres) of mixed conifer forests in the western United States (Anonymous 1981). Persistent defoliation by *C. occidentalis* has caused widespread growth loss and tree mortality in the United States and Canada. The adverse effects of western spruce budworm could be reduced through prediction of defoliation rates under given host and field conditions.

C. occidentalis is widely distributed throughout the mixed conifer forests of the western United States and Canada, from the southern edge of the Rocky Mountains in Arizona and New Mexico, north to British Columbia and west to Vancouver Island, Washington, and Oregon. Hosts of *C. occidentalis* include Douglas-fir (*Pseudotsuga menziesii* var. *glauca*[1]), true firs (*Abies* spp.), western larch (*Larix occidentalis*), and Engelmann spruce (*Picea engelmannii*). Trees of all ages are defoliated; new foliage is the preferred diet (Carolin and Honing 1972).

Defoliation by *C. occidentalis* injures the host trees by reducing the photosynthetic surface and interfering with transpiration and translocation within the trees. Defoliated trees may suffer growth loss, top kill, reduction of cone crops, and, if defoliation persists, death of the entire tree (Graham 1963, Kramer and Kozlowski 1960, Knight and Heikkenen 1980). The weakened host trees may also suffer from increased susceptibility to secondary insect pests (Knight and Heikkenen 1980).

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[1] Nomenclature of tree species after Little 1979.

Potential costs of these damages include loss of revenue for the forest industry, reduction of the timber resource, and possible diminished aesthetic and recreational value of the affected areas. Wildlife habitat may also be adversely affected by western spruce budworm infestations. The reduction of protective cover for deer and elk during cold winter months may result in mortality and depressed birthrates (Anonymous 1980a). Reduced food supplies for rodents and birds due to small cone crops may also result from forest defoliation (Duerr et al. 1975).

Information about factors that influence foliage consumption, foliage wastage, and nutritional efficiencies might enable the forest manager to predict the amount of defoliation that could occur based on given population levels. The ability to predict defoliation levels would contribute to the construction of appropriate integrated pest management systems for mixed confer forests throughout western North America. These pest management systems could be instrumental in reducing the considerable losses incurred from defoliation by the western spruce budworm.

Objectives

The specific objectives of this study were to determine:

1) feeding efficiencies of *C. occidentalis* on four species (i.e., Douglas-fir, white fir, corkbark fir, and Engelmann spruce).

2) differences in nutritional indices between vigor categories of the four host species.
3) seasonal variation in feeding efficiency and growth on two host species (white fir and Douglas-fir).
4) differences in nutritional efficiencies and consumptive rates between fourth, fifth, and sixth instar larvae on one host species (Douglas-fir) and on artificial diet.
5) differences in nutritional efficiencies and consumptive rates between budworm sexes on the four host species.
6) the amount of defoliation of the four host species due to foliage damaged but not consumed by the insects.

LITERATURE REVIEW

History of Outbreaks

In 1967, when the spruce budworm complex was revised, the western spruce budworm was first recognized as a separate species from the eastern spruce budworm, *C. fumiferana* Clemens (Stock and Castrovillo 1981). Before this, *C. occidentalis* was reported as part of the western complex of coniferous budworms of North America.

The first recorded outbreak of what is now called *C. occidentalis* occurred in southwestern Vancouver Island in 1909. Areas of serious defoliation continue to be prevalent through the host range in western British Columbia (Carolin and Honing 1972).

Defoliation by *C. occidentalis* was first recorded in the Pacific Northwest region of the United States in 1914 (Dolph 1980). *C. occidentalis* was first identified as a serious pest of mixed conifer stands in the western United States in 1922 when two outbreaks occurred in northern Idaho (Furniss and Carolin 1977). The area involved in this early outbreak was not recorded (Johnson and Denton 1975). Another outbreak was reported during the same year in Yellowstone National Park on Douglas-fir. At the time of the outbreak, entomologists estimated that the infestation had persisted since approximately 1919 (Johnson and Denton 1975).

Dolph (1980) described two major budworm outbreaks in Washington and Oregon. In 1943 an outbreak developed on the Okanogan National Forest in northeastern Washington. An estimated 80,972 ha (200,000 acres) were defoliated before the infestation collapsed from natural causes (i.e., adverse climate and starvation) in 1948. Another infestation developed in 1944 on the Umatilla National Forest in northeastern Oregon. The infestation eventually involved the entire fir host type throughout the Blue Mountains in northeast Oregon and southwest Washington.

Since 1947, when aerial detection surveys began in the Pacific Northwest, detailed information on *C. occidentalis* activity has been collected annually. Budworm damage has been continually reported except for the period of 1964 to 1969 in Oregon and 1965 to 1969 in Washington. Most of the defoliation activity has been located east of the Cascade Mountains (Dolph 1980).

Between 1948 and 1971 attacks by *C. occidentalis* were widely distributed across the Intermountain Region of the United States (Johnson and Denton 1975). In northern Idaho and Montana 4,098,077 ha (10,122,250 acres) of mixed conifer forests were infested. Between 1954 and 1971, 1,857,960 ha (4,589,160 acres) were infested in southern Idaho and Wyoming. Defoliation of mixed conifer stands by *C. occidentalis* continues to be a problem in these areas.

Defoliation by *C. occidentalis* has fluctuated widely in the southwestern United States. In 1977 total visible defoliation was estimated to be 80,076 ha (197,788 acres) in Arizona and New Mexico. Visible defoliation decreased to 31,796 ha (78,535 acres) in 1978 (Anonymous 1978) and increased in 1979 to approximately 53,036 ha (131,000 acres) (Anonymous 1979). *C. occidentalis* continued to cause extensive defoliation to mixed conifer stands throughout the Southwest in 1980, with the area of visible defoliation increasing to over 121,053 ha

(299,000 acres) (Anonymous 1980b). Areas of heaviest defoliation included the Kaibab National Forest and adjoining Grand Canyon National Park, Arizona, and the Carson, Santa Fe, and Cibola National Forests in New Mexico. During 1980, C. occidentalis defoliated approximately 1.65 million ha (4.08 million acres) of mixed conifer forests in the United States (Anonymous 1981).

Life Cycle

C. occidentalis generally completes its life cycle in 12 months with a small proportion of the population requiring 24 months to complete development (Carolin and Honing 1972). The adult moths are present in the field during late July and early August. The grey or orange-brown colored moths are approximately 12 mm in length with a wing span of 18 mm to 28 mm (Furniss and Carolin 1977). The adults of C. occidentalis are sluggish fliers but may be dispersed over great distances by air currents (McKnight 1968). The moths live approximately 5 days; flight and mating occur at dusk (Robertson 1979).

After mating, the females lay light-green, shingle-like egg masses on the underside of the needles. Each female lays approximately 150 eggs in masses averaging 25 to 40 eggs (Carolin and Honing 1972). The eggs hatch in 8 to 12 days (McGugan 1954).

The newly emerged larvae do not feed but instead seek suitable overwintering sites in bark fissures of their host tree. Here the first instar larvae molt, spin silken hibernating cases called hibernacula, and overwinter (Knight and Heikkenen 1980).

The termination of diapause is synchronized with the spring growth of the host trees. The second instar larvae emerge from their hibernacula and migrate to the foliage. The larvae then mine into the mature foliage where they feed for 7 to 14 days (Carolin and Honing 1972). If staminate flowers are available at this time, the young larvae prefer them to the mature foliage (Knight and Heikkenen 1980). The preference for staminate flowers is thought to be due to feeding stimulants, sugars, and the amino acid L-proline (McKnight 1968).

The larvae then leave the old foliage or staminate flowers and bore into the swelling vegetative buds. Within the protection of the buds the larvae feed on the tender expanding needles (Furniss and Carolin 1977). When the buds open and the foliage unfurls, the larvae of _C. occidentalis_ tie the needles and branch tips together to form protective feeding nests. Within the nests the larvae feed on the immature foliage, entirely destroying this resource before feeding on the mature foliage (Furniss and Carolin 1977). The larvae reach maturity 30 to 40 days after attacking the vegetative buds.

Pupation occurs within the feeding nest, or in a new web spun for pupation, in early to middle July. The coarctate pupae are 12 mm to 16 mm in length and change from light to dark brown during the 7 (Carolin and Honing 1972) to 10 (McKnight 1968) day pupal period.

The adult moths of _C. occidentalis_ emerge in late July and early August; adult males emerge a few days earlier than female moths. The sex ratio is approximately 50:50 (McKnight 1968).

Host Species Variation

Although there have been many studies on host preference by phytophagous insects, very little data has been reported on the feeding preference of _C. occidentalis_. Sang (1959) suggested that host preference may be based on the ability of insects to utilize diets that show a similar ability to support larval growth. He proposed that low food intake may be offset by high digestibility or high utilization of food for growth, and that poor digestibility may be offset by the efficient utilization of digested food. Waldbauer (1968) supported Sang in his suggestion that among some leaf-feeding insects digestibility and efficiency of conversion vary with the species of host plant.

Soo Hoo and Fraenkel (1966) suggested that for a host plant to be an adequate food source all necessary nutrients for the insects' growth must be present in the proper concentrations and proportions. They also found indications of dissimilarities in the nutritional value of leaves of different plant species, and suggested these dissimilarities may be a reason for differential feeding by an insect on its hosts. Waldbauer (1968) proposed that leaves of the same host may vary in their nutritional value.

Host preference has been studied for *C. fumiferana*, a species closely related to *C. occidentalis*. Durzan and Lopushanski (1968) found that the total amount of free amino acid was far greater in larvae fed balsam fir foliage than in spruce-fed larvae. The greater concentrations were reflected in the greater weight of the fir-fed larvae.

Phenological characteristics of host species may contribute to insect preference. Koller and Leonard (1981) suggested that the early availability of balsam fir foliage in relation to other hosts of *C. fumiferana* may contribute to the apparent preference for this host. The same authors suggested that white spruce may be a desirable host because of its close growing, sharp needles which protect the larvae from predators and because of the abundant and productive quality of the food it provides.

Seasonal Variation

The quality of an insect's natural diet is generally thought to change through the growing season (Scriber and Slansky 1981, Furniss and Carolin 1977). This change in food quality may explain any differential feeding rates and efficiency of utilization by *C. occidentalis* as the growing season progresses.

Koller and Leonard (1981) stated that *C. fumiferana* exhibits above average consumption rates in relation to other leaf feeding insects. They felt the higher rates may be related to the relative ease with which immature foliage is ingested. They stated that the total dry weight consumption by *C. fumiferana* larvae is approximately 10 times the initial pupal dry weight. The dry weight consumption by other Lepidopteran defoliators which feed on mature foliage is only five to seven times the dry pupal weight.

Scriber and Slansky (1981) suggested that a decline in nitrogen and leaf water content with tree foliage age contributes to the generally low efficiency of digestion and conversion by tree foliage feeders relative to forb feeders. Indeed, they found that nitrogen and leaf water content, under laboratory conditions, can be used to predict the upper limits for larval efficiencies. Finke (1977), as cited by Scriber and Slansky (1981), proposed that seasonal declines in nitrogen and leaf water content are more important than seasonal declines in secondary chemical concentrations in explaining digestion and conversion efficiencies.

Scriber and Slansky (1981) proposed that the attainment of the upper limit of larval performance may be inhibited by digestibility-reducing and other measurable host defenses which generally increase with foliage age. These defense mechanisms include increased content of lignin, silica, tannins, oils, waxes, and resins. This same study asserted that the quality and quantity of plant nutrients and allelochemics change through time and in response to environmental conditions.

Waldbauer (1968) suggested that total fresh weight consumption increases with the dilution of nutrients. In this manner the larvae partly compensate for a low nutrient concentration in their diet. If Scriber and Slansky (1981) are correct in their suggestion that nitrogen content is reduced as foliage age increases, then _C. occidentalis_ larvae should increase their food consumption as the growing season advances, up to the point where host defenses limit ingestion.

Heron (1964) suggested that hardening of the needles as host foliage reaches maturity may have a restrictive influence on larval feeding. He also stated that limited consumption of old needles by _C. occidentalis_ may also be due to the deterrent effects of appreciable amounts of pungenin in mature spruce needles. Ikeda et al. (1977) stated their belief that feeding deterrents are responsible for the seasonal feeding habits of many phytophagous insects.

Studies by Blais (1952, 1953) found that spruce budworm forced to feed on mature host foliage experienced reduced fecundity, retarded development, and increased mortality rates compared to those fed on the current year's growth. He concluded that the decrease in available current year foliage, resulting in the above conditions, may be a contributing factor in the collapse of epidemic populations. Heron (1964) concurred by stating that survival of spruce budworm is very poor if larvae are forced to feed on mature spruce needles throughout their development.

Instar Variation

Although knowledge of the consumptive rates and nutritional efficiencies among larval instars of C. occidentalis is lacking, information is available for immature insects as a whole and for a few specific insects. Davey (1954) suggested that the approximate digestibility (AD) and the efficiency of conversion (ECD) for immature insects declines with age. Scriber and Slansky (1981) suggested that a decline in AD with insect age is due to the consumption of less digestible fibers by later instars. In contrast, Kasting and McGinnis (1959) reported that AD remained constant for the pale western cutworm (Agrotis orthogonia Morrison) throughout larval development. Waldbauer (1968) stated that dry weight AD for the fall webworm (Hyphantria cunea Drury) feeding on boxelder (Acer negundo L.) increased during the 81 day larval period. Waldbauer also suggested that a decline in the efficiency of conversion of ingested food (ECI) by Bombyx spp. seems to be due to the decline in digestibility of foods, not to a decline in the efficiency of conversion of digested foods (ECD).

Scriber and Slansky (1981) reported that relative consumption rates, relative metabolic rates, and relative growth rates for immature insects tend to peak before or at the midpoint of an instar while daily utilization efficiency tends to decline as the instar progresses. They suggested that determination of efficiencies on a daily basis is less precise than on an instar basis because different amounts of food may be in the gut at different times during an instar. Koller and Leonard (1981) have found larvae of C. fumiferana to develop at a rapid rate from the beginning of the fourth instar through pupation, a period of 11.5 to 12.8 days. Dry weight of male larvae was said to increase 51 and 57 times on fir and spruce respectively during this period. Female dry weight increased 100 times during the same developmental period. They suggested that this rapid development is made possible by the high consumption rates of later instar larvae which compensates for low assimilation efficiency.

Scriber and Slansky (1981) supported Koller and Leonard's findings of increased growth and consumption rates during the penultimate and ultimate instars. They suggested that performance values calculated for these instars tend to be representative of those calculated for the entire larval stage of most insects.

Fast (1981) measured the needle surface area of balsam fir consumed by newly molted fourth instar larvae of C. fumiferana. He found the average surface area consumed to be 14.2 mm^2 with a standard error of ± 1.2 mm^2. Using these measurements he calculated average feeding rates of other larval instars. The average needle area consumed was calculated to be 2.4 mm^2 for a third instar larva, 29.0 mm^2 for a fifth instar larva and 194.0 mm^2 for a sixth instar larva. However, he cautioned that these areas consumed are approximate and most likely are different under forest conditions.

Host Vigor

Host vigor has been equated with site quality and has generally been acknowledged as a factor in tree susceptibility to insect attack. Williams et al. (1979) and Mason (1981) stated that Douglas-fir tussock moth (*Orgyia pseudotsuga* McDunnough) outbreaks tend to be associated with poor sites. Anderson (1944) found that vigorous trees were less attractive to bronzed birch borers (*Agrilus anxius* Gory). Blais (1958) thought the difference in tree vigor probably explained why low vigor (low quality site) trees offered less resistance to defoliation by *C. fumiferana* than high vigor (high quality site) trees.

The general health of host trees has also been related to the survival of the host trees and the insects that feed upon them. Furniss and Carolin (1977) asserted the belief that vigorous trees have a better chance of surviving insect attack than poor vigor trees. Mason (1981) stated that the site condition of the tree had no influence on the survival of the Douglas-fir tussock moth.

Insect Sex

The sex of an insect can also influence consumption rates and utilization efficiencies. Beckwith (1976) found that pupal weights for female Douglas-fir tussock moths were greater than for males. He also observed longer develoment times for females. Mukerji and Guppy (1970) observed that female armyworms (*Pseudaletia unipuncta* Haworth) generally consumed less corn foliage than males, but had higher ECI values and greater initial pupal weights.

Although food utilization has been studied for several insect species, no information is currently available on the consumption rate and nutritional efficiencies of the western spruce budworm. This insect is an important defoliator of mixed conifer stands in western North America. The defoliation results in growth loss and tree mortality as well as possible adverse affects on wildlife and aesthetic values in outbreak areas. Prediction and control of defoliation are necessary to reduce these impacts. Studies to measure the consumption rates and nutritional efficiencies of *C. occidentalis* are needed in order to make predictions of defoliation based on conditions in the field (i.e., host species, host vigor, host phenology).

CHAPTER 1

WESTERN SPRUCE BUDWORM CONSUMPTION - EFFECTS OF HOST SPECIES AND FOLIAGE CHEMISTRY

Introduction

Within a population of host plants, the intensity of insect attack and subsequent damage may vary considerably. It is not uncommon for two Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco, trees near each other to have quite different populations of western spruce budworm, *Choristoneura occidentalis* Freeman (McDonald 1981). Western spruce budworm (WSBW) frequently exhibits this preferential habit within and among its hosts in the Southwest.

Numerous explanations for preferential attack by insects have been suggested including differences in nutritional values, phenology, foliage toughness, host vigor, and plant defensive compounds. Foliage chemicals have been implicated as specific factors in the resistance-susceptibility characteristics of Douglas-fir (McMurray 1980). Literature on the important plant defensive compounds has been adequately reviewed by the following authors: tannins (Swain 1979), phenols (Levin 1971, Swain 1977), and nitrogen (Mattson 1980).

In this paper we present some preliminary results on WSBW feeding differences among the important hosts in the Southwest. We also report on correlations between WSBW feeding and concentrations of phenols, tannins, and proteins in white fir, *Abies concolor* (Gord. and Glend.) Lindl. ex Hildebr., and Douglas-fir foliage.

Methods

Tree Selection

Four hosts of WSBW occurring in northern Arizona were selected for the feeding experiments: Douglas-fir, white fir, corkbark fir, *Abies lasiocarpa* var. *arizonica* (Merriam) Lemm., and Engelmann spruce, *Picea engelmannii* Parry ex Engelm. Trees were selected from mixed conifer stands (2,400 - 2,500 m) approximately 16 km north of Flagstaff, Arizona.

Trees suitable for site index determination were rated for vigor according to Waring et al. (1980). This technique uses the ratios of the basal area growth for one-year and five-year increments to total sapwood area. To obtain average measurements, four increment cores were taken at 90° angles from each of 25 trees of each host species. The increment cores were then stained with potassium iodide-iodine to aid in distinguishing the sapwood from the heartwood (Kutscha and Sachs 1962). Total radius, sapwood radius, and one- and five-year increment radii were measured. The ratios were calculated using this formula:

$$\frac{BA_x}{SA} = \frac{R^2 \P - (R - r_x)^2 \P}{R^2 \P - (R - r_s)^2 \P}$$

BA_x: basal area of growth increment for period x

SA : sapwood area

R : total radius

r_x : radius of increment growth

r_s : radius of sapwood

Fifteen trees were selected from the 25 which were cored for each species (five trees in each of three vigor categories). The five trees with the highest ratios were classified as high vigor trees, the five trees with the lowest ratios were classified as low vigor trees, and the five trees closest to the mean were classified as medium vigor trees. The theoretical range of BA/SA ratio is 1.00 to 0.00. The actual range of BA_5/SA observed for the four species was: Douglas-fir 0.49 to 0.14, white fir 0.59 to 0.20, corkbark fir 0.63 to 0.24, and Engelmann spruce 0.60 to 0.13.

Selection of Larvae

Second and third instar larvae were collected in early May from an ongoing WSBW outbreak within the Kaibab National Forest, Arizona. Budworm infested branch tips were collected from the four host species used in this study. Larvae were carefully segregated according to host species; this allowed the larvae to be fed foliage from the same host species from which they were collected. The branch tips were placed in Aquapics® to maintain freshness and transported to the laboratory.

The field collected larvae were stored at 2-4°C to slow development until five to seven days before the experiments were to begin. The larvae were then placed at room temperature until they advanced to the fourth instar. Larvae were determined to be in the fourth stadium by head capsule measurements. Bean and Batzer(1957) and Wagg (1958) were used as guidelines.

Foliage Collection

To standardize the host phenological stage, feeding experiments were begun when the host foliage was determined to be at the "brush" stage (bud cap gone, needles even but no shoot growth so needles appear to arise from one spot) (R. Shepard unpublished).

We collected paired foliage samples at the four cardinal directions from the midcrown of the host trees. Paired twigs were selected for uniformity in size and phenology. One twig was fed to a budworm, the other twig was used to estimate the average dry weight per needle of the feeding twig. This average dry weight was later used to estimate the dry weight of the foliage consumed by the budworm larva.

Feeding Procedure

The paired twigs were saturated in a 100% relative humidity environment overnight. The following morning the mature foliage was trimmed from the feeding twig. While being held under water, the twig was excised and placed in a water-filled Aquapic®. The prepared foliage was then placed in a paper-lined 150 x 25 mm petri dish.

Fourth instar larvae were weighed fresh and placed on the prepared foliage to feed. Initial dry weight of each larva was estimated using an average percent dry weight of fourth instar larvae. The petri dishes were placed in controlled environmental chambers for the duration of the experiments. Temperature in the chambers ranged from 24 to 26°C; the photoperiod was 16 hours of light and 8 hours of darkness, as recommended by Robertson (1979).

Following each 72 hour feeding period the feeding twigs were removed and replaced with fresh foliage. The number of damaged needles was recorded and the damaged needles still attached to the twig as well as wasted needles were collected and oven dried at 60°C until no further weight loss occurred. Both wasted and remaining foliage were then weighed on a balance accurate to 0.1 mg. The amount of foliage ingested by each larva was estimated using the following formula:

$$I = (DW \times N) - (W + R)$$

I : foliage ingested

DW: mean dry weight per needle

N : number of needles damaged

W : foliage wasted (clipped but not consumed)

R : foliage remains (damaged but not clipped from the twig)

Each replicate was terminated within 24 hours of pupation. Total foliage ingested was calculated; pupae were sexed and weighed fresh. Feces and pupae were then oven dried at 60°C and weighed.

Nutritional indices were calculated on a dry weight basis according to Waldbauer (1968). The following nutritional indices are used in this study: foliage ingested (I), relative consumption rate (RCR), relative growth rate (RGR), approximate digestibility (AD), and efficiency of conversion of ingested food to body weight (ECI). A one-way analysis of variance (ANOVA) with alpha equal to 0.10 was used to analyze these data. The Least Significant Difference (LSD) multiple range test was used to determine where any differences occurred.

Chemical Analysis

Foliage used in the chemical analyses was clipped from the host trees selected for the feeding experiment and immediately frozen for 18 hours at -20°C. Samples were then freeze-dried at -50°C and 50 millitorr in a freeze dryer. Samples were stored at -20°C under dessication until analyzed.

Proteins were analyzed using the Coomassie Brilliant Blue Dye technique (Bradford 1976). Total phenols were determined using the Folin-Denis technique according to Swain and Hillis (1959) and Ribereau-Gayon (1972). Tannins were analyzed using the vanillin reaction assay (Price et al. 1978) as modified by W.V. Zucker (unpublished).

Results and Discussion

Comparison of Rearing Methods

The effect of three commonly used rearing procedures on fresh and dry female pupal weights was determined for WSBW feeding on Douglas-fir and corkbark fir. Fresh pupal weights were significantly different among rearing methods for corkbark fir but not for Douglas-fir (Table 1). For corkbark fir, fresh pupal weights were significantly higher for insects bagged on foliage in the field than for insects fed excised foliage in the lab. Excised foliage and bagged foliage tests were conducted on the same trees and crown positions. Fresh pupal weights were not significantly different between insects reared on excised foliage and insects that developed under normal field conditions for either host species. Dry weights of pupae were not significantly different between rearing methods (Table 2).

The technique of excising foliage for feeding experiments may lead to misleading results if inducible defensive mechanisms exist, because excised branches may not be able to respond to insect feeding by increasing concentrations of defensive compounds as would a normal branch. However, our study shows that feeding on excised foliage in the laboratory is probably a good approximation of feeding as it occurs under natural conditions. Bagging of insects on trees (white muslin

Table 1. Fresh pupal weights of female western spruce budworm by rearing method and host species

Rearing Method	Douglas-Fir (mg)	Corkbark Fir (mg)
Excised Foliage	70.6(5)[a/] A[b/]	69.0(5) A
Field Bagged	91.6(4) A	83.6(6) B
Field Collected	70.5(77) A	59.8(51) A
F-Prob.	0.1390	0.0014

[a/] numbers in parentheses are number of cases.

[b/] one-way ANOVA, LSD multiple range test, $\alpha = 0.10$, values followed by different letters are significantly different.

Table 2. Oven-dry pupal weights of female western spruce budworm by rearing method and host species

Rearing Method	Douglas-Fir (mg)	Corkbark Fir (mg)
Excised Foliage	20.8(5)[a/] A[b/]	19.2(5) A
Field Bagged	16.4(4) A	18.7(6) A
Field Collected	----	----
F-Prob.	0.4705	0.8974

[a/] numbers in parentheses are number of cases.

[b/] one-way ANOVA, $\alpha = 0.10$, numbers followed by different letters are significantly different.

bags) tends to increase pupal weights, probably as a result of reduced harassment from predators and parasites and because of micro-climate modification.

Influence of Host Species

A commonly held belief among foresters is that some host species are more resistant to both WSBW and eastern spruce budworm, *Choristoneura fumiferana* Clemens, than are other hosts. We compared the relative suitability of three of the important hosts in Arizona (Table 3). Pupal weights were not significantly different among the three hosts, which indicates that all hosts are a suitable substrate for insect development. Feeding efficiency (ECI) and growth rate (RGR) were significantly higher on Douglas-fir than on either white fir or corkbark fir. However, budworm larvae can apparently compensate for the lower quality of the foliage, as reflected in low ECI and RGR, by increasing their consumption rate (I) and probably the duration of the feeding period. This ability of insects to compensate for lower food quality by increasing consumption is often overlooked in studies of host plant-herbivore interaction. Too few replicates of Engelmann spruce were available to include in this analysis; however, qualitatively it appeared as if WSBW did quite well on spruce foliage when foliage is sufficiently developed at the time when WSBW normally begin feeding.

Chemical Content of WSBW Host Foliage

Current year's foliage of selected host trees was collected seven to 10 days after the beginning of the feeding studies. Foliage was collected from the same trees and crown position as those used in the feeding studies. Tannin concentration did not vary significantly

Table 3. Nutritional indices and pupal weights for western spruce budworm reared on three host species

Host	N	I	RCR	RGR	ECI	Pupal Weight[a]
Douglas-fir	13	185.0 A[b]	1.7 A	0.12 A	7.8 A	58.6 A
White fir	20	226.0 A	2.0 A	0.10 B	5.4 B	60.6 A
Corkbark fir	10	223.0 A	1.7 A	0.09 B	5.8 B	60.0 A
F-Prob.			0.163	0.012	0.003	0.957

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[a] pupal weight for male and female budworms are in mg fresh weight, all other weights based on mg dry weight.

[b] one-way ANOVA, $\alpha = 0.10$, LSD multiple range test, values followed by different letters are significantly different

between host vigor categories for any of the species tested (Table 4). Engelmann spruce had approximately twice the tannin content of any other host. Total phenols were not different among vigor categories for Douglas-fir and white fir (Table 5). However, medium vigor corkbark fir trees had lower total phenols than did the high or low vigor trees. Low vigor Engelmann spruce trees had lower total phenols than high and medium vigor trees. Protein content of foliage tended to decrease with host vigor for all host species tested (Table 6). However, this trend was statistically significant only for Engelmann spruce.

Relationship Between Foliage Chemistry and Insect Feeding

Pearson's correlation coefficients and a simple linear regression were used to evaluate the relationship between foliage chemistry and WSBW feeding. In each case foliage samples for chemical analysis and feeding were collected from the same aspect and crown position of the same trees. Only Douglas-fir and white fir are discussed here due to insufficient sample size for the other species.

Tannins in Douglas-fir were positively correlated with both foliage ingested and approximate digestibility (Table 7). These results were quite surprising considering that the theory of plant apparency (Feeny 1976, Rhoades and Cates 1976) would predict that the quality of the foliage and subsequent consumption should decrease as tannins increase. Phenols were not significantly correlated with any of the larval growth parameters studied. Protein was positively correlated with pupal weight. Adjusted R^2 values presented in Table 8 indicate

Table 4. Percent dry weight of tannins in western spruce budworm host foliage by host vigor class

Vigor	Douglas-Fir	White Fir	Corkbark Fir	Engleman Spruce
High	4.78 A[a]	5.64 A	4.51 A	9.12 A
Medium	3.91 A	4.58 A	4.98 A	9.71 A
Low	4.98 A	3.79 A	4.40 A	8.86 A
X	4.49	4.66	4.63	9.28

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[a] one-way ANOVA, $\alpha = 0.10$, LSD multiple range test, values followed by different letters are significantly different.

Table 5. Total phenol content of western spruce budworm host foliage by host vigor class [a/]

Vigor	Douglas-Fir	White Fir	Corkbark Fir	Engleman Spruce
High	0.11 A[b/]	0.07 A	0.19 A	0.12 A
Medium	0.10 A	0.06 A	0.13 B	0.13 A
Low	0.09 A	0.06 A	0.18 A	0.08 B
X	0.10	0.06	0.17	0.11

[a/] total phenols expressed in terms of absorbance per mg.

[b/] one-way ANOVA, $\alpha = 0.10$, LSD multiple range test, numbers followed by different letters are significant different.

Table 6. Percent dry weight of protein in western spruce budworm host foliage by host vigor class

Vigor	Douglas-Fir	White Fir	Corkbark Fir	Engleman Spruce
High	14.62 A[a/]	21.17 A	22.78 A	23.88 A
Medium	12.41 A	20.85 A	19.08 A	22.90 A
Low	11.69 A	17.47 A	19.86 A	16.77 B
X	12.86	19.93	20.57	21.36

[a/] one-way ANOVA, $\alpha = 0.10$, LSD multiple range test, numbers followed by different letters are significantly different

Table 7. Correlation coefficients indicating the relationship between Douglas-fir foliage chemistry and western spruce budworm larval growth parameters (n=7)

Foliage Chemicals	Larval Growth Parameters					
	Ingested	RCR	RGR	AD	ECI	Pupal Wt.
Tannins	0.72[a]	0.55	0.62	0.78[a]	-0.25	0.65
Phenols	0.26	-0.24	-0.37	-0.46	0.08	-0.38
Proteins	0.64	0.01	0.62	0.41	0.26	0.70[a]

[a] $P \leq 0.10$.

Table 8. Adjusted R^2 values for simple regression equations using Douglas-fir foliage chemicals to predict western spruce budworm larval growth (n=7) [a]

Foliage Chemicals	Larval Growth Parameters					
	Ingested	RCR	RGR	AD	ECI	Pupal Wt.
Tannis	0.40[b]	NS[c]	NS	NS	NS	NS
Phenols	NS	NS	NS	NS	NS	NS
Proteins	NS	NS	NS	NS	NS	0.57[b]

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[a] data transformed where appropriate to best fit the form of the relationship.

[b] $P \leq 0.10$.

[c] NS; not significant.

that leaf tannin content can be used to predict the amount of Douglas-fir foliage ingested and that protein content is a useful predictor of pupal weight.

The relationships between foliage chemicals and larval growth parameters for white fir were different from those observed for Douglas-fir. In this case tannins were negatively correlated with growth rate and efficiency (Table 9). This is consistent with the plant apparency theory. Adjusted R^2 values indicate foliage tannin content can be used to predict growth rate and efficiency (Table 10). Neither phenols nor proteins were correlated with any measure of larval growth for WSBW feeding on white fir foliage.

Douglas-fir, corkbark fir, white fir, and probably Engelmann spruce are all suitable host material for WSBW when current foliage flush is synchronized with the larval feeding period. Douglas-fir is of slightly better quality than the other species tested. However, because of the ability of the budworm to compensate for lower food quality by consuming more foliage, larvae can grow and develop quite well on lower foliage quality hosts. It is possible that white fir and corkbark fir could actually sustain more defoliation damage than Douglas-fir because their foliage is of lower quality. This is important to keep in mind when considering low foliage quality as a criterion for selecting resistant species or genotypes. In northern Arizona, Douglas-fir and true firs typically sustain more damage than Engelmann spruce, but this may be primarily because spruce is not phenologically synchronized with the feeding cycle of the WSBW.

There are suprisingly few differences in the tannins and phenols tested among vigor categories. Our study fails to show any evidence

Table 9. Correlation coefficients indicating the relationship between white fir foliage chemistry and western spruce budworm larval growth parameters (n=8)

Foliage Chemicals	Larval Growth Parameters					
	Ingested	RCR	RGR	AD	ECI	Pupal Wt.
Tannins	0.44	0.42	-0.68[a]	0.45	-0.85[a]	-0.22
Phenols	-0.28	-0.33	-0.38	-0.17	-0.37	-0.27
Proteins	0.18	0.14	0.15	0.12	0.13	0.25

[a] $P \leq 0.10$.

Table 10. Adjusted R^2 values for simple regression equations using white fir foliage chemicals to predict western spruce budworm larval growth (n=8) [a/]

Foliage Chemicals	Larval Growth Parameters					
	Ingested	RCR	RGR	AD	ECI	Pupal Wt.
Tannins	NS[b/]	NS	0.38[c/]	NS	0.64[c/]	NS
Phenols	NS	NS	NS	NS	NS	NS
Protein	NS	NS	NS	NS	NS	NS

[a/] data transformed where appropriate to best fit the form of the relationship.

[b/] NS; not significant.

[c/] $P \leq 0.10$.

that high vigor trees maintain higher levels of tannins and phenols than do low vigor trees. Nor is there any evidence to suggest that the technique of excising foliage, and presumably preventing induction of defensive compounds, enables insects to perform better than if they feed on a host which could actively defend itself. There may be differences in protein content between vigor categories, but even in the worst case (foliage with only 11% protein) there appears to be adequate protein to sustain insect development.

Differences in tannins, phenols, and proteins among species are more striking. Tannins are almost twice as abundant in Engelmann spruce as in the other species. But, considering the different relationship between tannins in white fir and Douglas-fir and feeding parameters, it is uncertain whether high tannin content has a negative or positive effect. There are differences in phenols between species but, here again, there is no apparent relationship to feeding parameters. Douglas-fir, which based on efficiency and growth rate of larvae is the best host, actually had the lowest average protein content of the host species tested.

Phenols do not appear to influence feeding by WSBW even though the phenolic content in budworm hosts is within the concentration range that has been reported to influence host selection by aphids (Zucker 1982).

The relationship between foliage tannins and some of the larval growth parameters is intriguing. It is likely that the tannins are not identical in Douglas-fir and white fir. But, the levels of tannins are well within the range found by Feeny and Bostock (1968) who argued that higher tannin content is related to lower food quality. Bernays (1981) suggests that tannins may actually be used as a nutrient source by grasshoppers. In Douglas-fir, tannins were positively correlated with digestibility. In white fir, tannins were negatively correlated with growth and efficiency. It is difficult to explain these apparently opposite results, except that tannins and proteins are intercorrelated in Douglas-fir which may result in a random correlation. Clearly we need to know more about the role of foliage tannins in larval feeding and growth in the WSBW.

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CHAPTER 2

THE INFLUENCE OF HOST VIGOR ON FEEDING AND DEVELOPMENT OF THE WESTERN SPRUCE BUDWORM, *CHORISTONEURA OCCIDENTALIS* FREEMAN, IN NORTHERN ARIZONA

Introduction

Host vigor, as a function of site quality and moisture availability, has long been associated with susceptibility to insect attack (Knight and Heikkenen 1980, Furniss and Carolin 1977, Anderson 1944). Mason (1981) and Williams et al. (1979) stated that Douglas-fir tussock moth, *Orgyia pseudotsuga* McDonnough, outbreaks tend to be associated with low quality sites and high moisture stress. Blais (1958) found trees growing on low site quality plots offered less resistance to defoliation by the spruce budworm, *Choristoneura fumiferana* Clemens, than trees growing on high site quality plots.

Contrary to these prevailing beliefs, insect outbreaks also occur on favorable sites where trees are healthy and vigorous. DeLeon (1954) has asserted that the cause of most outbreaks is a change in the health and size of the attacking insect population, rather than the vigor of the host trees or their growing condition. DeLeon's theory has not gained credibility among forest entomologists nor has it received much attention as an opposing view in the literature.

The purpose of this study was to evaluate the influence of host vigor, as determined by the Waring et al. (1980) technique for vigor estimation, on feeding and development of the western spruce budworm, *Choristoneura occidentals* Freeman, in northern Arizona. Waring et al. (1980) estimate tree vigor based on studies by Gordon and Larson (1968), Rangnekar and Forward (1973), and Fogel and Hunt (1979) which show that stemwood production has less priority in the carbon budget of trees than root and shoot growth. Therefore, the proportion of carbon allocated to stemwood production should be a measure of tree vigor (Waring et al. 1980). The specific objectives of this study were to evaluate consumption rates, food utilization, foliage wastage, development time, and fresh pupal weights of *C. occidentalis* in relation to the estimated vigor of four host species in northern Arizona.

Methods

Tree selection, feeding procedure, and nutritional indices calculations follow those of Wagner and Blake (1983). Four trees from each vigor category (i.e., high, medium, and low) were selected from each of three host species, Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco), white fir (*Abies concolor* [Gord. and Glend.] Lindl. ex. Hildebr.), and corkbark fir (*Abies lasiocarpa* var. *arizonica* [Meriam] Lemm.). Ratios of one and five year increments of growth to total sapwood area (BA_1/SA and BA_5/SA, respectively) were calculated for each host species and divided into high, medium, and low vigor categories (Table 1).

Second and third instar larvae were collected in the field from an ongoing outbreak of *C. occidentalis* within the Kaibab National Forest, Arizona. The collection area was approximately 16 km north of Grand Canyon National Park at approximately 2652 meters (8700 feet) in elevation. The larvae were segregated according to the host species

Table 1. Vigor rating for host trees[a/] used in 1982 feeding experiment

Host	High Vigor			Medium Vigor			Low Vigor		
DF	Tree #	BA_1/SA	BA_5/SA	Tree #	BA_1/SA	BA_5/SA	Tree #	BA_1/SA	BA_5/SA
	8	.49	.49	1	.31	.26	16	.27	.22
	7	.52	.45	12	.30	.30	15	.17	.14
	6	.48	.41	5	.33	.29	14	.25	.21
	20	.39	.39	11	.35	.26	18	.25	.22
				9	.28	.26			
WF				10	.07	.33	2	.03	.20
	20	.15	.59	5	.07	.30	19	.05	.24
	9	.11	.55	17	.07	.33	18	.05	.26
	1	.10	.43	6	.08	.35	15	.05	.24
CBF	5	.72	.61	20	.50	.42	11	.28	.28
	10	.63	.63	19	.50	.38	8	.30	.25
	6	.62	.50	18	.39	.42	21	.35	.24
	16	.61	.61	9	.39	.39	14	.35	.33

[a/] DF = Douglas-fir, WF = white fir, CBF = corkbark fir.

from which they were collected, allowing the larvae to be fed foliage of the same host species during the experiments. The larvae were transported to the laboratory and allowed to advance to the fourth instar. Fourth instar larvae, which appeared to be healthy, were selected for the feeding experiments using head capsule measurments (Bean and Batzer 1957 and Wagg 1958).

Experiments began when the current year's foliage of each host reached the 'brush' stage (Shepard unpublished) to standardize the phenological stage of the host foliage used in the experiments. Paired foliage samples were collected at the four cardinal directions from the midcrown of the selected host trees. One twig was fed to a budworm, the other twig was used to estimate the average dry weight (DW) per needle of the feeding twig. Budworms were placed on the foliage and allowed to feed until pupation. Twigs were replaced every 72 hours. The experiments were conducted with a photoperiod of 16-8 (light-dark) and temperatures of 24-26 °C.

Each replicate was terminated within 24 hours of pupation. The pupae were sexed and weighed fresh for comparison of fresh pupal weight. Pupae and total feces from each replicate were oven dried at 60°C until no further weight change could be detected. Foliage ingested by each larvae was summed, percent foliage wasted was determined, and the duration of the replicate was noted. Detailed methods used in these experiments are outlined in Wagner and Blake (1983).

Nutritional indices were calculated on a dry weight basis according to Waldbauer (1968). Categorical host vigor data were analyzed for each host species using a one-way analysis of variance (AOV) with alpha equal to 0.10. The Least Significant Difference (LSD) multiple range test was employed to determine where any differences occurred.

The influence of host vigor category on total ingested foliage (I), relative consumption rate (RCR), relative growth rate (RGR), and efficiency of conversion of ingested foods to body weight (ECI) are reported. Development time (T), fresh weight of pupae (F.W. pupae), and the percent of damaged foliage wasted (foliage wasted) are also reported by vigor category for each species. The latter is important because the amount of foliage wasted by C. occidentalis is part of the total defoliation damage.

Data from each host species were also analyzed with the vigor ratios treated as continuous data. Only BA_5/SA was used for these analyses. Pearson's correlation test was used to determine if the nutritional indices were correlated with vigor for each of the three host species tested. Regression analyzes were used to determine the predictive value of host vigor for the significantly correlated nutritional indices.

Results and Discussion

Categorical Data

The influence of host vigor category on food consumption and utilization by C. occidentalis feeding on Douglas-fir foliage is summarized in Table 2. None of indices reported were significantly affected by host vigor category in this experiment. Results were identical for budworms feeding on white fir foliage (Table 3).

Fresh pupal weight was the only utilization measure which was significantly influenced by host vigor category in the experiment using

Table 2. The influence of host vigor categories on food consumption and utilization by C. occidentalis feeding on Douglas-fir foliage

Vigor Category	Food Utilization Indices I	RCR	RGR	ECI	F.W. Pupae
High (9)[b]	187.86 A[a]	1.53 A	0.12 A	8.41 A	68.84 A
Medium (2)	165.40 A	1.80 A	0.12 A	7.26 A	58.55 A
Low (2)	190.10 A	2.07 A	0.12 A	5.60 A	68.85 A
F-Prob.	.7843	.3199	.8609	.2940	.7675

[a] one-way ANOVA, $\alpha = 0.10$, LSD mulitple range test, values followed by different letters are significantly different.

[b] numbers in parentheses are number of cases.

Table 3. Influence of host vigor categories on food consumption and utilization by *C. occidentalis* feeding on white fir foliage

Vigor Category	Food Utilization Indices				
	I	RCR	RGR	ECI	F.W. Pupae
High (8)[b]	270.28 A[a]	1.99 A	0.10 A	5.24 A	68.00 A
Medium (5)	173.86 A	1.86 A	0.12 A	6.10 A	58.98 A
Low (7)	226.46 A	2.04 A	0.10 A	5.08 A	53.24 A
F-Prob.	.2025	.8588	.5011	.5859	.4299

[a] one-way ANOVA, α = 0.10, LSD mulitple range test, values followed by different letters are significantly different.

[b] numbers in parentheses are number of cases.

corkbark fir foliage (Table 4). Because I, RCR, RGR, and ECI were statistically equal for budworms in the three vigor categories, these data suggest that, in order for the fresh pupal weight to be significantly different, the initial weights of the fourth instar budworms were different between the categories. The heavier fresh pupal weights of budworms feeding on low vigor category corkbark fir foliage may also be due to them all being females. According to findings of Blake and Wagner (unpublished) female western spruce budworm pupae are significantly heavier than males. This is supported by Scriber and Slansky (1981) who state that female insects are generally heavier than males, a fact which is probably due to reproductive strategy. Fresh pupal weights of the budworms feeding on foliage from high vigor category trees were based on weights from male budworms only. This category had the lowest average fresh pupal weight. The medium vigor category had fresh pupal weight which were between the high vigor category and low vigor category values. The average fresh pupal weight for the medium vigor category was based on two male and one female budworm. Because of the uneven sex ratio within the experiment using corkbark fir, the significance of the fresh pupal weights is questionable. The fresh pupal weights of budworms feeding on Douglas-fir and white fir are based on both male and female budworms in each host vigor category.

The average development times and percent foliage wasted by vigor category for Douglas-fir, white fir, and corkbark fir are presented in Table 5. Development times were not significantly different between vigor categories for any of the host species tested. Development time of budworms feeding on high and low vigor category corkbark fir foliage

Table 4. The influence of host vigor category on food consumption and utilization by *C. occidentalis* feeding on corkbark fir foliage

Vigor	Food Utilization Indices				
Category	I	RCR	RGR	ECI	F.W. Pupae
High (3)	223.37 A[a]	2.06 A	0.08 A	4.52 A	43.87 A
Medium (3)	186.73 A	1.59 A	0.09 A	5.91 A	61.03 AB
Low (4)	249.35 A	1.38 A	0.09 A	6.67 A	71.33 B
F-Prob.	.7124	.4588	.5109	.2727	.0213

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[a] one-way ANOVA, $\alpha = 0.10$, LSD mulitple range test, values followed by different letters are significantly different.

[b] numbers in parentheses are number of cases.

Table 5. Influence of vigor category on development time (T), in days and precent of damage foliage wasted by C. occidentalis feeding on three host species

Vigor Category	Host Species Douglas-Fir T	 Foliage Wasted	 White Fir T	 Foliage Wasted	 Corkbark Fir T	 Foliage Wasted
High	13.56 A[a/]	17.94 A	15.00 A	12.35 A	15.67 A	19.50 A
Medium	12.50 A	13.85 A	12.80 A	19.39 A	13.00 A	12.13 A
Low	11.50 A	5.48 A	14.71 A	20.59 A	15.25 A	19.43 A
F-Prob.	.7696	.2678	.4297	.1947	.6461	.3488

[a/] one-way ANOVA, α = 0.10, LSD mulitple range test, values followed by different letters are significantly different.

was expected to be significantly different because of sexual segregation. However, this did not occur. The percent of damaged foliage that was wasted by C. occidentalis was not significantly different between the vigor categories for the three host species tested.

Continuous Data

Some nutritional indices of the western spruce budworm were found to be significantly correlated with host vigor at $P \leq 0.10$ when host vigor ratios were treated as continuous data (Table 6). RGR was positively correlated with vigor for budworms feeding on Douglas-fir foliage. The correlation coefficient (r) was 0.4069, however, the R^2 value was only 0.0953. ECI was significantly correlated with host vigor with r equal to 0.4306. The R^2 was 0.2907 which indicates that host vigor is a fair predictor of ECI for budworms feeding on Douglas-fir foliage. I, RCR, and fresh weight of pupae were not significantly correlated with host vigor for Douglas-fir.

ECI of budworms feeding on white fir foliage was positively correlated with tree vigor. The correlation coefficient was 0.3962 with a corresponding R^2 of 0.2024, indicating that host vigor is not a strong predictor of ECI even though they are correlated. The four other indices reported were not found to be correlated with white fir tree vigor at $P \leq 0.10$.

RCR, RGR, ECI, and fresh pupal weight were significantly correlated with the vigor of corkbark fir trees. RCR had an r of 0.4498 and an R^2 value of 0.2024. Even though RCR was positively correlated with host vigor, vigor was not a very good predictor of RCR. RGR was negatively

Table 6. Correlation coefficents indicating the relationship between host vigor ratios and nutritional indices for C. occidentalis feeding on Douglas-fir, white fir, and corkbark fir foliage

Host Species	Nutritional Indices				
	I	RCR	RGR	ECI	F.W. Pupae
Douglas-Fir (13)[a]	.2254	-.2679	.4069[b]	.4306[b]	.1994
White Fir (18)	-.0014	-.2137	.2699	.3962[b]	.2112
Corkbark Fir (10)	-.0635	.4498[b]	-.5957[b]	-.6605[b]	-.8611[b]

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[a] numbers in parentheses are number of cases.

[b] $P \leq 0.10$.

correlated with vigor (r=-0.5957); therefore, as host vigor increased RGR decreased. The R^2 was 0.3366, indicating that host vigor is a fair predictor of RGR. ECI was also negatively correlated with host vigor. Its r value was -0.6605 with an R^2 of 0.4014. Fresh pupal weight for budworms feeding on corkbark fir foliage had a strong negative correlation with tree vigor (r=-.8611). The R^2 value was 0.7415, indicating that host vigor a good predictor of pupal weights of budworms feeding on corkbark fir foliage. However, due to the uneven sex distribution in the corkbark fir experiment, no definite conclusions can be reached.

Conclusions

The results of the categorical analysis of the influence of host vigor on food consumption and utilization by C. occidentalis feeding on Douglas-fir, white fir, and corkbark fir appears to contradict the generally accepted theory of susceptibility to insect attack. The only significant difference in budworm utilization performance was found in the fresh pupal weights of budworms feeding on corkbark fir foliage. This difference may be real or it may be the result of the apparently random success of only female budworms on low vigor foliage and only male budworms on high vigor foliage during this experiment. According to Blake and Wagner (unpublished) female budworms have significantly greater pupal weights than male budworms. Therefore, the significant difference in fresh pupal weights found between budworm feeding on high and low vigor corkbark fir foliage may be due to sex rather than host vigor.

Because development time and foliage wasted were not significantly different between vigor categories for the three host species tested, any observed disparity in the amount of defoliation damage can not be attributed to these factors. Nor can host vigor be implicated as the cause of slow development or increased foliage wasting by _C. occidentalis_.

Analysis of host vigor as continuous, rather than categorical data, appears to be a more appropriate test of the influence of host vigor on budworm feeding. Correlations do exist between vigor and budworm feeding, but they do not appear to be as strong as is generally thought. Host vigor was found to be a fair predictor of RGR and ECI, but the correlations were not consistent in their relationship for different host species.

Results of this study may be questioned because of the feeding technique used. Clipping foliage from the trees may turn off any inducible defense mechanisms of the hosts. However, Wagner and Blake (1983) compared the fresh pupal weights of western spruce budworm larvae reared on clipped foliage and larvae reared in the field on bagged branches and found no significant differences between the feeding techniques. Thus, the technique of clipping foliage to feed the larvae in the laboratory appears to be valid for the western spruce budworm.

Another problem with these results is the low number of successful replicates. The loss of replicates was primarily due to parasitism by two hymenopterans, _Apanteles_ spp. and _Glypta_ spp. which parasitize eggs and early instar larvae of _C. occidentalis_. Percent parasitism is presented by host species from which the larvae were collected in Table 7.

Table 7. Percent parasitism by two hymenopteran parasites on *C. occidentalis* in northern Arizona

Host	Percent of Total Samples Parasitized	Percent of Parasitized Samples by Each Species	
		Apanteles spp.	*Glypta* spp.
DF[a]	33.33	18.75	81.24
WF	43.75	9.00	90.48
CBF	68.75	22.92	66.67

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[a] DF = Douglas-fir, WF = white fir, CBF = corkbark fir.

Experiments were begun with 48 replicates for each of the three host species tested. Thirty-three percent of the budworms feeding on Douglas-fir foliage were found to be parasitized. Of the 33 percent, *Apanteles* spp. emerged from 19 percent of the parasitized larvae, *Glypta* spp. emerged from 81 percent. White fir replicates sustained a 44 percent parasitism rate, with nine percent of the total parasitized by *Apanteles* spp. and 91 percent by *Glypta* spp. Sixty-nine percent of the corkbark fir replicates were parasitized. *Apanteles* spp. emerged from 23 percent and *Glypta* spp. emerged from 67 percent of the total parasitized corkbark fir replicates. Because the budworms were selected at random from within their host groups, these parasitism rates probably represent the percent of parasitism occurring within the budworm population on the Kaibab National Forest.

No definite conclusions can be made from this study. However, based on our results, the theory that low vigor trees are more susceptible to insect attack than are high vigor trees may not hold true for the western spruce budworm. *C. occidentalis* may have evolved its early spring emergence to avoid physical or chemical host defenses which may develop later in the growing season and which may be influenced by the vigor of the host tree. This would explain why western spruce budworm attacks have been observed on seemingly vigorous trees. Perhaps DeLeon's (1954) theory that insect population quality is more important than host vigor is indeed valid for predicting outbreaks of *C. occidentalis* and other early season insect defoliators.

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CHAPTER 3

NUTRITIONAL INDICES OF WESTERN SPRUCE BUDWORM, *CHORISTONEURA OCCIDENTALIS* FREEMAN - EFFECT OF SEX AND INSTAR

Introduction

Defoliation by western spruce budworm, *Choristoneura occidentalis* Freeman, larvae is due to both foliage ingested and foliage clipped from the stem but not ingested. This damage may be influenced by instar or sex. Although the affect of these variables on consumption and utilization has been studied for a small number of insect defoliators, few studies have specifically examined their influence on *C. occidentalis*.

The influence of larval instar on nutritional indices has been studied for *C. fumiferana* Clemens, the eastern spruce budworm. Koller and Leonard (1981) found that *C. fumiferana* develops rapidly from fourth instar through pupation. They suggested this may be due to high consumption rates during the later instars, which may compensate for a low assimilation efficiency. Fast (1981) measured the surface area of balsam fir, *Abies balsamea*, foliage consumed by newly molted fourth instar *C. fumiferana*. The larvae consumed an average 14.2 mm^2 of foliage. Fast then calculated the surface area consumed by third instar (2.4 mm^2), fifth instar (29.0 mm^2) and sixth instar larvae (194.0 mm^2). His conclusions agree with Scriber and Slansky (1981) who state that the consumption rate of immature insects increases during the penultimate and ultimate instars.

Consumption rates and utilization efficiencies have been shown to be influenced by sex for some insect species. Female armyworms, *Pseudaletia unipuncta* Haworth, consume less corn foliage than males, yet they are greater in both conversion efficiency and initial pupal weight (Mukeryi and Guppy 1970). Beckwith (1976) observed longer development times and greater pupal weights for female Douglas-fir tussock moths, *Orgyia pseudotsuga* McDunnough, than for males.

The purpose of this study was to determine the influence of larval instar (fourth, fifth, and sixth) and sex on food consumption and utilization by the western spruce budworm.

Methods

Budworm larvae were collected from four host species (Douglas-fir, *Pseudosuga menziesii* var. *glauca* [Beissn.] Franco; white fir, *Abies concolor* [Gord. and Glend.] Lindl. ex. Hildebr.; corkbark fir, *A lasiocarpa* var. *arizonica* [Merriam] Lemm.; and Engelmann spruce,(*Picea engelmannii* Parry ex. Engelm.) within an outbreak on the Kaibab National Forest, Arizona. The larvae were segregated by host species and transported to the laboratory. Healthy fourth instar larvae were selected for the experiments from each host group. Instar was determined using head capsule measurements reported by Bean and Batzer (1957) and Wagg (1958).

Trees of the same host species from which the larvae were collected were used to provide foliage for the experiments. The trees were located approximately 16 km north of Flagstaff, Arizona. Foliage was collected at the four cardinal directions from the midcrown of the trees and brought to the laboratory. Mature foliage was removed and the twigs were placed in Aquapics® to maintain foliage freshness. Foliage was replaced every 72 hours. The experiments were conducted under controlled environmental condition of 16 hours of light and eight hours of dark and 24-26 °C.

Foliage ingested and percent foliage wasted were calculated for each replicate (see Wagner and Blake 1983). Nutritional indices were calculated on a dry weight basis following Waldbauer (1968). Detailed methods for tree selection, foliage and larvae collection, feeding procedure, and calculation of nutritional indices are reported by Wagner and Blake (1983).

Sex

Fourth instar larvae were placed on the prepared foliage and allowed to feed until pupation. At termination pupae were sexed and weighed to compare fresh pupal weights of male and female budworms. Pupae and feces were then oven-dried at 60°C until no further weight loss occurred and then weighed. Nutritional indices were calculated and data were analyzed using a one-way analysis of variance (AOV), with alpha equal to 0.10, to determine if there were differences in food consumption and utilization between male and female budworms.

Instar

Variation among larval instars was examined using larvae collected in the field, which were fed host foliage, and laboratory reared larvae, which were fed a commercially available artificial diet. Comparisons were made among instars within and between larval source groups.

Foliage-fed larvae. One medium vigor Douglas-fir tree was selected as the foliage source for this experiment. Fourth, fifth, and sixth instar larvae were weighed and placed in individual 150 x 25 mm petri dishes and allowed to feed on the foliage for three days. At termination each larva was weighed fresh, oven-dried along with its feces, and weighed again. The initial oven-dry weight for each fourth instar larva was calculated using an average percent oven-dry weight for fourth instar larvae. Initial dry weight was calculated for each fifth and sixth instar larva using its own final percent oven-dry weight. A one-way AOV was used to analyze the nutritional data with alpha equal to 0.10. The Least Significant Difference (LSD) multiple range test was used to determine where any differences occurred.

Artificial diet-fed larvae. A non-diapausing, laboratory-reared strain of *C. occidentalis* was obtained from the Pacific Southwest Forest and Range Experiment Station, Berkeley, California. The larvae were reared from eggs on artificial western spruce budworm diet.

Using head capsule measurements fourth, fifth, and sixth instar larvae were chosen for the experiment. Larvae were weighed and placed on pre-weighed cubes of artificial diet. Other cubes were used to determine the average percent dry weight of the artificial diet. This percent was used to calculate the initial dry weight of each feeding cube.

Feeding was terminated after three days. Larvae were weighed fresh and larvae, feces, and the feeding cube remains were oven-dried. The samples were weighed and the amount of ingestion food (I) and the nutritional indices were calculated. The amount of ingested food was calculated as follows:

$$I = (F \times D_A) - D_W$$

where I = food ingested in mg dry weight

F = initial fresh weight of the diet cube

D_A = average percent dry weight of diet cubes

D_W = final dry weight of the diet cube

Data were analyzed using a one-way AOV and an LSD multiple range test; alpha was equal to 0.10. The comparison of each instar by larval source was analysed using a one-way AOV with alpha equal to 0.10.

Result and Discussion

Nutritional indices reported here include food ingested (I), relative consumption rate (RCR), relative growth rate (RGR), efficiency of conversion of ingested food to body weight (ECI), development time (T), fresh pupal weight, and foliage wasted (percent of damaged foliage that was not consumed. Development time and fresh pupal weight are applicable only to the sex experiment. Foliage wasted is expressed for the experiments where foliage was used for feeding.

Sex

Sex had a significant influence on consumption and utilization of host foliage. Female budworms ingested more foliage during their feeding period than did males (Table 1). However, males had a higher RCR and an RGR equal to that of females. Although there was no statistically significant difference in ECI values, female budworms were more efficient, with an ECI of 7.09, than were males, whose ECI was

Table 1. Difference in ingestion and food utilization of western spruce budworm between sexes

Sex	I	RCR	RGR	ECI
Male[1]	188.37 A[2/3]	1.91 A	.11 A	6.02 A
Female	255.09 B	1.48 B	.10 A	7.09 B
F-Prob.	.0058	.0129	.3292	.1092

[1] n = 30 males and 16 females.

[2] oneway AOV, $\alpha = 0.10$.

[3] values followed by different letters are significantly different.

6.02. These data indicate that C. occidentalis females were able to maintain an RGR equal to that of males while consuming smaller amounts of foliage in relation to their body weight. This may be due to their slightly greater ECI.

Development time, in days, from fourth instar through pupation, foliage wasted, and fresh pupal weights are shown in Table 2. Females had a significantly longer development time than males, perhaps explaining why females ingested more foliage than did males during the experiment. C. occidentalis larvae wasted the same percent of foliage regardless of sex. Because female larvae had a longer development time than male larvae, these data indicate that female larvae wasted a smaller percentage of foliage per day.

The fresh pupal weight of female budworms was greater than that of males. Female pupae weighed an average 69 mg while male pupae weighed only 56 mg. These results are not surprising in light of the longer development time and greater foliage ingestion, as well as the egg producing role of the female budworm. Interestingly, the fresh pupal weights for the western spruce budworm were lower than those of the eastern spruce budworm, which is a closely related species of Choristoneura.

Instar

Foliage-fed larvae. The results of the experiment using larvae collected in the field were based on a small sample size. Loss of replicates was primarily due to insect parasites which had attacked the budworms before they were collected. Fourth instar was represented by only one sample, therefore it was omitted from the statistical analysis.

Table 2. Development time, percent of damaged foliage wasted, and initial fresh pupal weight of western spruce budworm by sex

Sex (mg)	Development Time (days)[1]	Foliage Wasted (%)	Fresh Pupal Weight
Male[2]	12.93 A[3][4]	18.22 A	56.87 A
Female	15.81 B	17.17 A	69.57 B
F-Prob.	.0026	.6906	.0270

[1] photoperiod: 16-8 L-D, temperature: 24-26°C.

[2] n = 30 males and 16 females.

[3] oneway AOV, $\alpha = 0.10$.

[4] numbers followed by different letters are significantly different.

The nutritional indices for fifth and sixth instar larvae are presented in Table 3. Sixth instar larvae ingested significantly more foliage than did fifth instar larvae, but RCR, RGR, and ECI were equal. Because the relative utilization indices were not different for the two instars tested, these data indicate that sixth instar larvae must ingest more food in order to maintain their greater weight and body size.

Although the percentage of foliage wasted by fifth instar larvae was greater than that of sixth instar larvae, the difference was not statistically significant. Therefore, the increase in the amount of defoliation by sixth instar larvae can be directly attributed to an increase in the amount of foliage ingested.

Artificial diet-fed larvae. The experiment using laboratory reared larvae feeding on artificial diet included fourth instar larvae and produced different results than the previous experiment (Table 4). Fourth instar larvae ingested less food than either fifth or sixth instar larvae, which had statistically equal I's. This contrasts with the foliage-fed larvae which ingested significantly less food during the fifth instar than during the sixth instar. RCR of fourth instar larvae was greater than for fifth and sixth instars. These data indicate that the fifth and sixth instar larvae fed artificial diet weighed approximately the same amount. RGR was higher for fourth and fifth instar than for sixth instar larvae, and ECI of fourth instar larvae was lower than those of fifth and sixth instar, which were statistically equal. The implications are that fourth instar larvae have a higher RCR to compensate for their lower ECI in comparison to fifth and sixth instar larvae. The significant difference in the RGR of sixth instar

Table 3. Relationship of western spruce budworm instar and food consumption and utilization, using natural foliage

Instar	I	RCR	RGR	ECI	% Foliage Wasted
Fifth (5)[2]	41.84 A[1]	3.08 A	0.18 A	6.80 A	20.34 A
Sixth (9)	76.46 B	3.01 A	0.22 A	9.30 A	11.78 A
F-Prob.	.0306	.8992	.4700	.1960	.3028

[1] one-way AOV, $\alpha = 0.10$, numbers followed by different letters are significantly different.

[2] numbers in parentheses are number of cases.

Table 4. Relationship of western spruce budworm larval instar and food consumption and utilization, using artificial diet

Instar	I	RCR	RGR	ECI
Fourth (13)[2]	31.25 A[1]	3.62 A	0.32 A	9.24 A
Fifth (15)	56.97 B	1.35 B	0.28 A	20.62 B
Sixth (13)	62.32 B	1.08 B	0.21 B	18.80 B
F-Prob.	.0000	.0000	.0112	.0000

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[1] one-way AOV, α = 0.10, LSD multiple range test; numbers followed by different letters are significantly different.

[2] numbers in parenthesis are number of cases.

larvae feeding on artificial diet as compared to fifth instar larvae does not agree with the data from larvae feeding on natural foliage. Average weight and weight gained during the feeding period are used to calculated RGR. The high standard deviation of these variables about their respective means in the artificial diet experiment as compared to the foliage experiment may explain the discrepancy between the results.

Comparison of foliage-fed and artificial diet-fed larvae. No comparison was made with fourth instar larvae due to the lack of adequate replication in the experiment using natural foliage. There were differences between fifth instar larvae (Table 5). The larvae feeding on artificial diet ingested more food but had a lower RCR value than larvae feeding on foliage. This indicates that diet-fed larvae were larger than the foliage-fed larvae. Both RGR and ECI were significantly lower for foliage-fed larvae than for diet-fed larvae. These data indicate that larvae feeding on artificial diet were able to grow at a faster rate than foliage-fed larvae due to their greater ECI. The results of comparing sixth instar larvae are shown in Table 6. Foliage-fed larvae maintained an RGR statistically equal to diet-fed larvae by consuming more food in relation to their body size. This high RCR offset the low ECI of foliage-fed larvae.

Laboratory-reared larvae feeding on artificial diet appear to have an advantage in food utilization over larvae feeding on foliage. The nutritionally balanced, easily digested artificial diet, ideal environmental conditions, and lack of pressure from parasites and predators, especially in the early instars, allowed laboratory-reared larvae to be more efficient feeders and to gain more weight due to less

Table 5. Comparison of food comsumption and utilization by fifth instar larvae feeding on natural foliage and artificial diet

Diet	I	RCR	RGR	ECI
Foliage (5)[2]	41.84 A[1]	3.11 A	0.20 A	6.84 A
Artificial Diet (15)	56.97 B	1.35 B	0.28 B	20.62 B
F-Prob.	.0718	.0000	.0990	.0000

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[1] one-way ANOVA, $\alpha = 0.10$, numbers followed by different letters are significantly different.

[2] numbers in parentheses are number of cases.

Table 6. Comparison of food consumption and utilization by sixth instar larvae feeding on natural foliage and artificial diet

Instar	I	RCR	RGR	ECI
Foliage (9)[2]	76.46 A[1]	3.06 A	0.28 A	9.34 A
Artificial Diet (13)	62.32 A	1.08 B	0.21 A	18.80 B
F-Prob.	.2245	.0000	.1451	.0015

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[1] one-way ANOVA, $\alpha = 0.10$, numbers followed by different letters are significantly different.

[2] numbers in parenthesis are number of cases.

energy expenditure than their field-collected counterpart which fed on foliage.

Conclusions

The results of our study generally concur with the comprehensive review by Scriber and Slansky (1981). They state that mature female larvae and pupae tend to be heavier than males due to some combination of longer development time, during which they consume more food, and faster RCR, I, or ECI if both sexes have the same initial weight. *C. occidentalis* females have a longer growing period than do males, allowing them to ingest greater total foliage, have a higher ECI, and attain greater weight than males. Scriber and Slansky suggest that the differences in nutritional performance by male and female insects may be due to reproductive strategies. The end results of longer development times and greater total ingestion of foliage by female budworms is greater defoliation damage to host trees.

There is little difference in the food utilization by fifth and sixth instar *C. occidentalis* feeding on natural foliage. There is an increase in the amount of food ingested by sixth instar larvae which can probably be attributed to the need to maintain an increased body weight. Larvae feeding on artificial diet follow the same general pattern but have a lower RCR, probably due to their plentiful nutritious food source. If the comparisons resulted in positive correlations between the larval strains, then the laboratory-reared larvae could be used in lieu of field larvae.

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CHAPTER 4

FOLIAGE PHENOLOGY AS A FACTOR IN FOOD UTILIZATION BY THE WESTERN SPRUCE BUDWORM, *CHORISTONEURA OCCIDENTALIS* FREEMAN

Introduction

The nutritional quality of tree foliage for insect herbivores is thought to decline through the growing season (Furniss and Carolin 1977; Scriber and Slansky 1981). Scriber and Slansky (1981) propose that the generally low efficiency of digestion and conversion by tree foliage feeders may be due to a decline in nitrogen and leaf water content with foliage age. Waldbauer (1968) states that total fresh weight consumption increases with the dilution of nutrients. Larval feeding performance may also be inhibited by digestability-reducing chemicals, as well as other measurable host defenses, which generally increase with foliage age (Scriber and Slansky 1981). If nitrogen content decreases with foliage age, then *C. occidentalis* Freeman larvae should compensate for the decrease by increasing their food consumption as the growing season advances, up to the point where host defenses limit ingestion.

The seasonal feeding habit of many phytophagous insects may be influenced by feeding deterrents (Ikeda et al. 1977). Heron (1964) asserts that the limited consumption of mature spruce needles by *C. occidentalis* larvae may be due to the inhibitory effect of appreciable amounts of pungenins in the needles. He also suggests that larval feeding may be restricted by the hardening of needles as the foliage matures. Both *C. occidentalis* and *C. fumiferana* Clemens, the eastern spruce budworm, experience reduced fecundity, retarded development, and high mortality rates when forced to feed on mature spruce foliage throughout their development (Heron 1964, Blais 1952, 1953).

The purpose of this study was to determine the influence of host phenology on food consumption and utilization by the western spruce budworm in northern Arizona.

Methods

Feeding experiments were conducted in June and August of 1981 and again in June and July of 1982. Host tree and larval selection, and calculation of nutritional indices followed Wagner and Blake (1983). Collection of larvae and foliage, preparation of foliage for feeding, and calculation of ingested foliage differed in 1981 and 1982.

1981 Feeding Experiment

When *C. occidentalis* larvae were collected in the field, no attempt was made to segregate them based on the host foliage from which they were collected. Third instar larvae were selected for the first seasonal experiment using head capsule measurements (Bean and Batzer 1957; Wagg 1958). The remaining larvae were reared to pupation, mated, and allowed to oviposite. when the eggs hatched, the larvae were placed on artificial diet to feed. Those larvae which did not diapause were reared to the fourth instar and used for the second seasonal feeding experiment.

Foliage was collected at random from the lower crown of Douglas-fir, Pseudotsuga menziesii var. glauca [Beissn.] Franco, corkbark fir, Abies lasiocarpa var. arizonica [Merriam] Lemm., and Engelmann spruce, Picea engelmannii Parry ex. Engelm. trees located approximately 16 km north of Flagstaff, Arizona. Previous year's needles were clipped from the stem; the twigs, with current year's foliage attached, were then weighed.

The foliage twigs were changed every 72 hours and the foliage twigs which had been fed upon were weighed. Fresh weight of foliage ingested was calculated as follows:

$$W_I = W_B - W_A$$

where: W_I = weight of foliage ingested in mg

W_B = weight of the foliage twig before feeding in mg

W_A = weight of the foliage twig after feeding in mg

Oven-dry weight was estimated for each twig using the percent oven-dry weight (60°C until no further weight loss occurred) of an aliquot twig.

Each replicate was terminated at pupation or when the larva stopped feeding. Pupae and total feces for each replicate were oven-dried and then weighed. Total foliage ingested was calculated and duration was noted for each replicate. Data were analyzed using a one-way analysis of variance (AOV) with alpha equal to 0.10.

1982 Feeding Experiment

Foliage and larvae collection, foliage preparation, and calculation of ingested foliage follow Wagner and Blake (1983). Larvae used for the second seasonal experiment were placed in cold storage at the time of collection to slow their development. Larvae were brought to room temperature five days before the second seasonal experiment was to begin and allowed to advance to the fourth instar.

Each replicate was terminated at pupation or when feeding ceased. Total foliage ingested was calculated; pupae and feces were oven-dried and then weighed. After calculating the nutritional indices, data were analyzed using a one-way AOV, with alpha equal to 0.10, to determine if there were differences in budworm feeding between early and middle season foliage.

Results and Discussion

Total foliage ingested was eliminated from the data analysis because the length of feeding time was highly variable between the feeding seasons. All of the larvae feeding on early, or normal, season foliage reached maturity, while larvae feeding on middle (1982) and late (1981) season foliage died before reaching pupation. Although all of the larvae used in the second seasonal experiments died, the nutritional indices were still calculated for the period during which they fed.

Results of the 1981 experiment using Douglas-fir foliage showed significant differences between early and late season foliage for all the nutritional indices (Table 1). Budworms feeding on late season foliage appear to have increased their relative consumption rate (RCR) to compensate for a decrease in efficiency of conversion of ingested food to body weight (ECI). Despite this effort, *C. occidentalis* larvae were unable to maintain a relative growth rate (RGR) statistically equal to budworms feeding on early season foliage.

C. occidentalis larvae feeding on Engelmann spruce foliage followed the same pattern of food utilization (Table 2). Although their average

Table 1. Effect of Douglas-fir foliage phenology on food utilization by western spruce budworm (1981)

Season	Food Utilization Indices		
	RCR	RGR	ECI
Early (4)[b]	3.00 A[a]	0.09 A	5.08 A
Late (4)	9.28 B	0.01 B	0.16 B
F-Prob.	.0726	.0162	.0116

[a] one-way AOV, $\alpha = 0.10$, values followed by different letters are significantly different.

[b] numbers in parentheses are number of cases.

Designations apply for all following tables.

Table 2. Effect of Engelmann spruce foliage phenology on food utilization by western spruce budworm (1981)

Season	Food Utilization Indices		
	RCR	RGR	ECI
Early (3)	1.33 A	0.15 A	11.65 A
Late (2)	4.19 B	-0.05 B	-1.34 B
F-Prob.	.0097	.0050	.0072

RCR increased significantly, the larvae lost weight due to a significant decrease in ECI.

Table 3 presents the results of the feeding experiment using corkbark fir foliage. Although no significant differences were found for the three indices reported, the pattern of change in food utilization remains the same as for Douglas-fir and Engelmann spruce.

Results of the 1982 early and middle season feeding experiment are presented in Table 4. Significant differences were found in utilization between early and middle season feedings. RGR and ECI decreased significantly, which follows the pattern of the 1981 experiment. RCR decreased significantly during the middle season feeding rather than increasing as would be predicted by Waldbauer (1968). This outcome was an unexpected inconsistency with the results of the 1981 analysis of RCR.

Conclusions

Host foliage phenology appears to greatly influence the food utilization and developmental success of C. occidentalis. Although no chemical tests were conducted on the foliage used for these experiments, the significant changes in RCR, RGR, and ECI suggest that chemical and physical changes may be occurring during the growing season. As predicted by Waldbauer (1968) and Scriber and Slansky (1981), RCR was significantly greater and ECI was significantly lower for budworms feeding on late season foliage than those feeding on early season foliage in 1981. Despite this effort to compensate for a sub-optimal food source, the budworm larvae were unable to complete their development.

Table 3. Effect of corkbark fir foliage phenology on food utilization by western spruce budworm (1981)

Season	Food Utilization Indices		
	RCR	RGR	ECI
Early (2)	2.67 A	0.13 A	4.78 A
Late (5)	4.70 A	0.06 A	3.24 A
F-Prob.	.4974	.2410	.5551

Table 4. Influence of Douglas-fir foliage phenology on food utilization by western spruce budworm larvae (1982)

	Food Utilization Indices		
Season	RCR	RGR	ECI
Early (6)	1.58 A	0.08 A	5.08 A
Middle (2)	1.05 B	-0.08 B	-8.02 B
F-Prob.	.0191	.0002	.0014

In 1982 RCR was significantly different between the seasons tested, but the difference was the inverse of the 1981 experiment. The low RCR indicates that the larvae may have encountered feeding deterrents or physical barriers to feeding. The low RCR could also be due to the period of cold storage used to slow larval development. Development may have been retarded to the point where the larvae could not recover.

Budworm feeding on middle and late season foliage experienced retarded development and high mortality rates. None of the larvae used for the middle and late season experiments survived to pupation, though many fed as long as the successful larvae feeding on early season foliage. These findings are consistent with those of Heron (1964) who studied _C. occidentalis_ feeding on mature white spruce needles.

The feeding behavior of _C. occidentalis_ appears to be adapted for making the most of the nutrients provided by its hosts' foliage early in the growing season, while avoiding the physical and chemical defenses that may increase as the foliage matures. Studies of the physical and chemical changes in the foliage of these host trees as the growing season progresses are needed to better understand the feeding behavior of the western spruce budworm.

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SUMMARY

This study investigated some of the factors influencing the feeding behavior of the western spruce budworm on host species in northern Arizona. Factors studied included host species, foliage chemistry, host vigor, larval instar, sex, and foliage phenology.

All host species tested were suitable for larval development. Pupal weight was statistically equal for all hosts, but the amount of foliage necessary for successful development was less for budworms feeding on Douglas-fir. Therefore, Douglas-fir trees probably suffer less defoliation damage per budworm than do corkbark fir and white fir trees. However, Douglas-fir may suffer greater or equal amounts of total defoliation because these trees can support more budworms on their high food quality foliage.

Host vigor was not a reliable predictor of the feeding success of *C. occidentalis*. Any chemical or physical defenses which may be influenced by tree vigor were not apparent in the food utilization indices used in this study. Therefore, any attempt to increase the vigor of host trees would not significantly affect their susceptability to defoliation by *C. occidentalis*.

The amount of foliage ingested increased with budworm instar. This was attributed to an increase in body size with each succeeding instar. Sex also influenced the amount of foliage ingested. Female budworms ingested more foliage due to their longer development time. These results indicate that direct control methods should be implemented

as early as possible in the growing season in order to reduce the total amount of defoliation damage to host trees.

C. occidentalis was able to successfully complete its development only on early season immature foliage. As the foliage matured, larval development was retarded and mortality increased. If synchrony of bud burst and larval emergence could be interrupted, budworm populations, and therefore defoliation, could be decreased significantly.

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